FLORISTIC DIVERSITY AND COMPOSITION OF TERRA FIRME AND SEASONALLY INUNDATED PALM SWAMP FORESTS IN THE PALMA REAL WATERSHED IN LOWER MADRE DE DIOS, PERU

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ABSTRACT

We report the results of a tree species inventory of seven hectares of lowland subtropical moist forest in the Palma Real River watershed of lower Madre de Dios, Peru, where we discovered a type of palm swamp forest vegetation that has not previously been studied. The goal of the study was to investigate the forest vegetation of the Palma Real watershed with special emphasis on a comparison between the wetland forest vegetation and the surrounding terra firme forests. A total of 3534 trees ≥10 cm DBH belonging to 442 species in 62 families were measured and identified in the seven plots. Three distinct forest types resulted from Principal Components Analysis (PCA) and WPGMA cluster analysis of both family and species abundance data, including two types of terra firme forests and a palm swamp forest. The five terra firme forest plots sampled, with a range of 104–138 species, were less diverse than other one-hectare forest plots reported from the region, which have a diversity ranging from 151-197 species. The two palm swamp forest plots, with 126 and 167 tree species, were more diverse than surrounding terra firme forest plots sampled in this study. One of the palm swamp forest plots was extremely diverse with 167 species, only seven species less than the average diversity across 14 one-hectare terra firme plots sampled by other investigators in Madre de Dios, Peru. Both palm swamp forest plots had a greater number of stems distributed across smaller size classes. Both Fabaceae and Arecaceae were the most important plant families across all plots. The Arecaceae contributed significantly to distinguishing the palm swamp forest plots, composing 16–25% of all stems compared to only 9% of the stems in terra firme plots of the region. This high abundance of the palm family is from where we derive the name we are applying to this wetland forest type in the Palma Real watershed. Using satellite imagery we illustrate the importance of the extent of these palm swamp forests throughout the region.

RESUMEN

Reportamos los resultados de un inventario floristico de siete hectáreas en un bosque subtropical húmedo en la cuenca de la quebrada Palma Real, en Madre de Dios, Perú. El objetivo de este estudio fue investigar la vegetación de la Quebrada Palma Real con especial énfasis en una comparación

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entre un tipo de vegetación de pantano con palmeras y la vegetación de terra firme circundante. En total de 3534 árboles mayores a 10 cm de diametro (DAP) pertenecientes a 442 especies en 62 familias fueron medidos e identificados en siete parcelas. Tres tipos de bosque resultaron de los análisis de componentes principales y análisis de agrupamiento WPGMA mediante datos de abundancia por familia y por especie en los dos tipos de vegetación. Las cinco parcelas muestreadas en terra firme, con un rango de 104–138 especies por parcela, fueron menos diversas que otras parcelas estudiadas en la región, las cuales tienen un rango de 151–197 especies. Las dos parcelas muestreadas en bosque pantanoso de palmeras, con 126 y 167 especies, fueron más diversas que las parcelas de terra firme circundantes. Una de las parcelas del bosque pantanoso de palmeras fue extremadamente diversa con 167 especies, solo siete especies menos que el promedio reportado para 14 otras parcelas estudiadas por otros investigadores en Madre de Dios. Ambas parcelas del bosque pantanoso con palmeras tuvieron una alta densidad de tallos distribuidos en las clases diamémetricas más pequeñas, lo cual podría ser una explicación de la alta diversidad de especies. Fabaceae y Arecaceae fueron las familias más importantes para todas las parcelas. Arecaceae contribuyó significativamente a distinguir el bosque pantanoso con palmeras, comprendiendo entre el 16–25% de todos los tallos, comparado con solo el 9% de tallos en bosque de terra firme de la region. Esta alta abundancia de palmeras determinó el nombre que nosotros aplicamos a este tipo de bosque muy húmedo en la cuenca de la Quebrada de Palma Real. Usando imágenes satelitales nosotros ilustramos la importancia por su extensión, de estos bosques pantanosos de palmeras en la región. Finalmente nosotros instamos a desarollar mas estudios de largo plazo sobre la diversidad y ecología en la región, con énfasis en la importancia de estos bosques de Palma Real en la extracción de castaña (*Bertholletia excelsa*, Lecythidaceae) y otros recursos para la región y sus moradores.

INTRODUCTION

A large forest plot network has accumulated in the last decade from the Amazonian region. The highest tree species diversity has been reported from the western Amazon where Gentry (1988) and Valencia et al. (1994) recorded 283 and 307 species respectively in one-hectare forest plots. Oliveira and Mori (1999) found 285 species per hectare on very poor soils and under reduced rainfall in central Amazonia, which is essentially the same species diversity as found by Gentry in western Amazonia. In an analysis of data from 97 existing one-hectare forest plots from the Amazon, including the Guiana Shield, Ter Steege et al. (2000) showed that in all regions terra firme forests harbor a greater number of tree species per unit than any other forest types. Patterns of high tree species diversity have been attributed to high rainfall and more nutrient-rich soils of the western Amazon (Gentry 1988).

Nebel et al. (2001) and Kvist and Nebel (2001) emphasize the importance of wetland forests to both the ecological diversity and resource use in the Peruvian Amazon. While many forest plot inventories in the Amazon have focused on the diversity of terra firme and floodplain forests, few studies in the region have dealt with wetland vegetation. For example, only two swamp forest plots from the Amazon were available for inclusion in the large studies by Ter Steege et al. (2000, 2003), but those were excluded from the final analyses and spatial modeling. There is clearly a lack of data from wetland habitats in the Amazon. This minimal coverage of wetland vegetation leads to a generalized view of the complexity and diversity of these ecosystems, as discussed by Kalliola et al. (1991), who argue for more focused studies.

The Tambopata-Candamo region and Manú National Park are two well-studied protected areas of Madre de Dios, Peru, that hold world records in diversity of various organisms, such as birds, insects, and mammals. National reserves, such as Tambopata, allow for protection and sustained use of plant resources. The Palma Real watershed is inside the Tambopata National Reserve and the Bahuaje-Sonene National Park, where management plans are needed since plant and animal extraction is carried out by indigenous and local people. Yet, no floristic treatment exists for the region and only a few small areas are represented by checklists.

In the Palma Real watershed and the surrounding region, there exists a vast area of terra firme forest and patches of seasonally inundated swamp forests. This mosaic of forests extends from the Tambopata Reserved Zone of lower Madre de Dios, Peru, to the Pampas del Heath in the border region of Peru and Bolivia. The seasonally inundated forests of this region are characterized by a distinctive topography that consists of small raised islands separated by shallow water channels during the rainy season or heavy rains in the dry season, and they sit upon a deep, fine, heavy gray soil. Because of the abundance of palm species in our study area we refer to this wetland vegetation as palm swamp forest. We have reviewed available literature that relates to the diversity, ecology, and distribution of wetland vegetation in the area, and we have found no existing description of this specific wetland vegetation. The palm swamp forests of Palma Real are different in species and family diversity and composition than the palm swamp forest communities of the northern Peruvian Amazon described by Kalliola et al. (1991). Although Haase (1990) described palm swamp communities in northern Bolivia, there is no description that matches the palm swamp forests of the Palma Real watershed. Nor are these palm swamp forest communities covered by Beck (1984). The goal of this study was to investigate the forest vegetation of the Palma Real watershed in lower Madre de Dios, Peru, with special emphasis on a comparison between these palm swamp forests and the surrounding terra firme forest vegetation.

METHODS

Study Site

The study was conducted in the Palma Real watershed, a tributary of the Madre de Dios River, approximately 28 km to the southeast of Puerto Maldonado, the capital and the principal city of the Department of Madre de Dios, Peru (Fig. 1). Nested within the Tambopata-Candamo National Reserve and the Bahuaje-Sonene National Park, this area of lowland subtropical moist tropical forest (Foster et al. 1994) receives about 2208 mm of precipitation annually and the average temperature is 24°C (mean over 36 years). During the driest months, May to

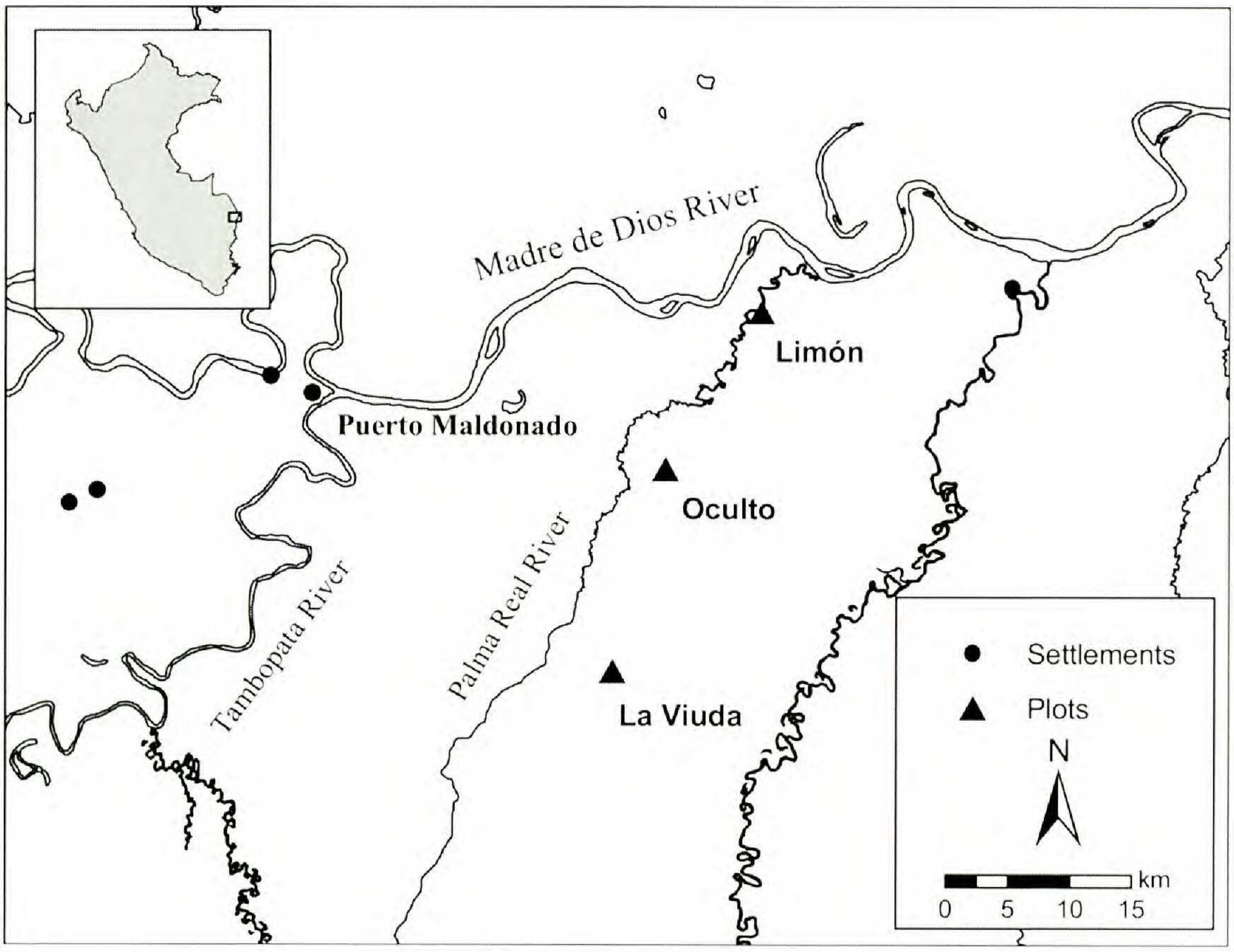

Fig. 1. Location of the three sites where forest plot studies were based, Limón, Oculto, and La Viuda.

September, the area receives occasional cold winds from the antarctic, which decreases daily temperatures to a minimum of 7–8°C, although this phenomenon of cold fronts, known as "friajes", lasts for only a few days at a time.

The general topography is flat, dissected by small streams, most of which are without water during the dry season. Three main types of habitats exist in the Palma Real watershed, forming an interesting mosaic of vegetation zones: (1) high terrace non-inundated forest (terra firme); (2) palm swamp forests - areas with poor drainage and seasonal inundation causing the formation of swamp-like forests; and (3) seasonally inundated floodplain forest. This study focused on terra firme and palm swamp forests, which are the most extensive forest types in the study area. The Brazil nut tree (*Bertholletia excelsa*, Lecythidaceae) is abundant in large areas of the terra firme forests in this region but it is absent from others. Seeds of the Brazil nut tree are extracted from the Palma Real watershed by harvesters (castañeros) every year during January–March, making this an economically important region in Madre de Dios, Peru. The forests of the Palma Real watershed maintain a healthy fauna with jaguars, ocelots, tapirs, peccaries, deer, and at least six species of monkeys. No logging activities have been conducted in this region since twenty years ago when many Spanish Cedar trees (*Cedrela odorata*, Meliaceae) were extracted. Then terra firme forests of Palma Real that are characterized by high Brazil nut tree density have been divided by the Peruvian government into forest concessions of approximately 1000 hectares each and given to local extractors living in Puerto Maldonado.

Soils.—The soils of the terra firme forests are dominated by red clay and those of palm swamp forests by gray clay. Within the Palma Real zone, three representative sites were selected for quantitative studies of floristic diversity and composition (Figs. 1, 6): (1) Limón (12°32'19"S; 68°51'40"O), close to the Madre de Dios River; (2) Oculto (12°39'03"S; 68°55'40"O), in the middle of the zone; and (3) La Viuda (12°47'43"S; 68°58'07"O), to the extreme south of the zone.

Field Data

Seven permanent one-hectare forest plots were established in the Palma Real watershed, divided between Limón (3 plots), Oculto (3 plots) and La Viuda (1 plot). Within each site, one plot was established in terra firme (TF) forest with a known high density of 5–7 individuals of Brazil nut trees per hectare (Limón 1, Oculto 1, La Viuda 1). One plot in each of Oculto and Limón was established in TF forest with known absence of Brazil nut trees (Oculto 2 and Limón 2). In Oculto and Limón one plot was also established in palm swamp (PS) forest (Oculto 3 and Limón 3).

Each plot consisted of a square area of 100 × 100 m, divided into 25 subplots of 20 × 20 m. Each corner of the one-hectare forest plot is marked with a PVC stake labeled with the respective X,Y coordinate in red paint. All individuals, including palms, 10 cm or greater in diameter at breast height (DBH) were measured, mapped and identified to family, genus, and species or morphospecies when definite species determination was not possible. All individuals with multiple stems were considered as one individual, and the diameters of each stem were summed for basal area calculations.

Every species is represented by duplicate voucher specimen collections of one or more individuals. All identifications were made in the La Molina Herbarium (MOL) at the Agraria University in Lima, Peru, where duplicate voucher specimens were deposited. The Cronquist system of classification of flowering plants was used for the purposes of this project.

Data Analysis

Relative diversity, relative density, and relative dominance were calculated for each plot. The Importance Value Index (IVI) was calculated at the species and family level for each plot using the sum of the three measures, relative diversity, relative density, and relative dominance. Sørensen Similarity Index (Sørensen 1948) was calculated for all species found in the plots and for the 20 most abundant species. The Sørensen index is $2 * S_{12} / (S_1 + S_2)$, where S_{12} is the number of species common to both sites and S_1 and S_2 are the total number of species found at site one and two. Plots were also grouped based on species and family abundance using Principal Components Analysis (PCA) and WPGMA cluster analysis (MVSP 3.12, Kovach Computing Services).

Comparing the raw number of species between plots without accounting for differences in stem density can give misleading results. To avoid this problem we used individual based rarefaction curves as suggested by Gotelli and Colwell (2001). Rarefaction curves were calculated using the software package EstimateS 7.5 (Colwell 2005).

RESULTS

Forest Structure

A total of 3534 trees ≥10 cm DBH belonging to 442 species in 62 families were measured and identified in the seven plots (Table 1). Three distinct forest types resulted from PCA: (1) palm swamp forest (Limón 3 and Oculto 3); (2) Limón terra firme forest (Limón 1 and Limón 2); and (3) Oculto/La Viuda terra firme forest (Oculto 1, Oculto 2 and La Viuda) (Figs. 2, 3). PCA resulted in almost no difference between the species (Fig. 2) and family level (Fig. 3), a pattern previously suggested by Terborgh and Andersen (1998).

Table 1 shows the principle structural characteristics for each plot. The palm swamp (PS) forests (PS) in both Limón and Oculto have a higher number of species than the terra firme (TF) forests at the same sites. Limón 3 has the highest number of individuals and species of all the plots while the two TF forest plots at Oculto are the least diverse. The rarefaction curves (Fig. 4) confirm these results and show that the higher diversity of the PS forest plots are not simply due to a higher stem density. The PS plots have a lower basal area than the TF plots (21.5 vs. 27.3). Distribution of trunk diameter classes shows the inverse J-shaped curve, with a mean proportion of 69% of individual trees found between 10 and 20 cm DBH.

Composition

Monimiaceae was the most abundant family in the TF forest plots, followed by Arecaceae and Fabaceae (Table 2). In PS forest plots Arecaceae and Fabaceae were the most abundant families. Looking at the 20 most abundant families (Table 2), Lauraceae, Moraceae, Violaceae, Lecythidaceae, Chrysobalanaceae, Sapotaceae, Burseraceae, and Cecropiaceae were found in both TF and PS forests, whereas Myristicaceae, Strelitziaceae, Linaceae, Bixaceae, Rubiaceae and Flacourtiaceae were found only in TF forests. Of the 20 most abundant families, Myrtaceae, Dichapetalaceae, Anacardiaceae, Clusiaceae, Ochnaceae, Sterculiaceae, and Combretaceae were restricted to the PS forests. The ten most abundant families represented 64% of all individual trees found. The most species-rich family across all plots was Fabaceae, followed by Lauraceae, Moraceae, Sapotaceae, Chrysobalanaceae, and Annonaceae. The ten richest families represented 54%

TABLE 1. Structural characteristics from 1 hectare plot.

	Limón 1	Limón 2	La Viuda	Oculto 1	Oculto 2	Oculto 3	Limón 3
No. of stems	499	532	473	422	508	492	608
No. of species	138	130	130	109	104	126	167
Basal area (m^2)	32.23	23.77	25.23	29.25	26.22	21.86	21.07
Categories by diameter (%)							
10–20 cm	63.4	70.5	69.5	64.9	65.9	74.6	74.5
20.1–40 cm	27.6	23.5	22.2	23.0	24.8	20.3	21.9
40.1–80 cm	7.4	5.1	7.0	10.2	8.3	4.3	3.5
> 80 cm	1.6	0.9	1.3	1.9	1.0	0.8	0.2
No. of species in 50% IVI	16	16	18	13	13	14	20
No. of families in 50% IVI	39	42	41	41	40	42	45

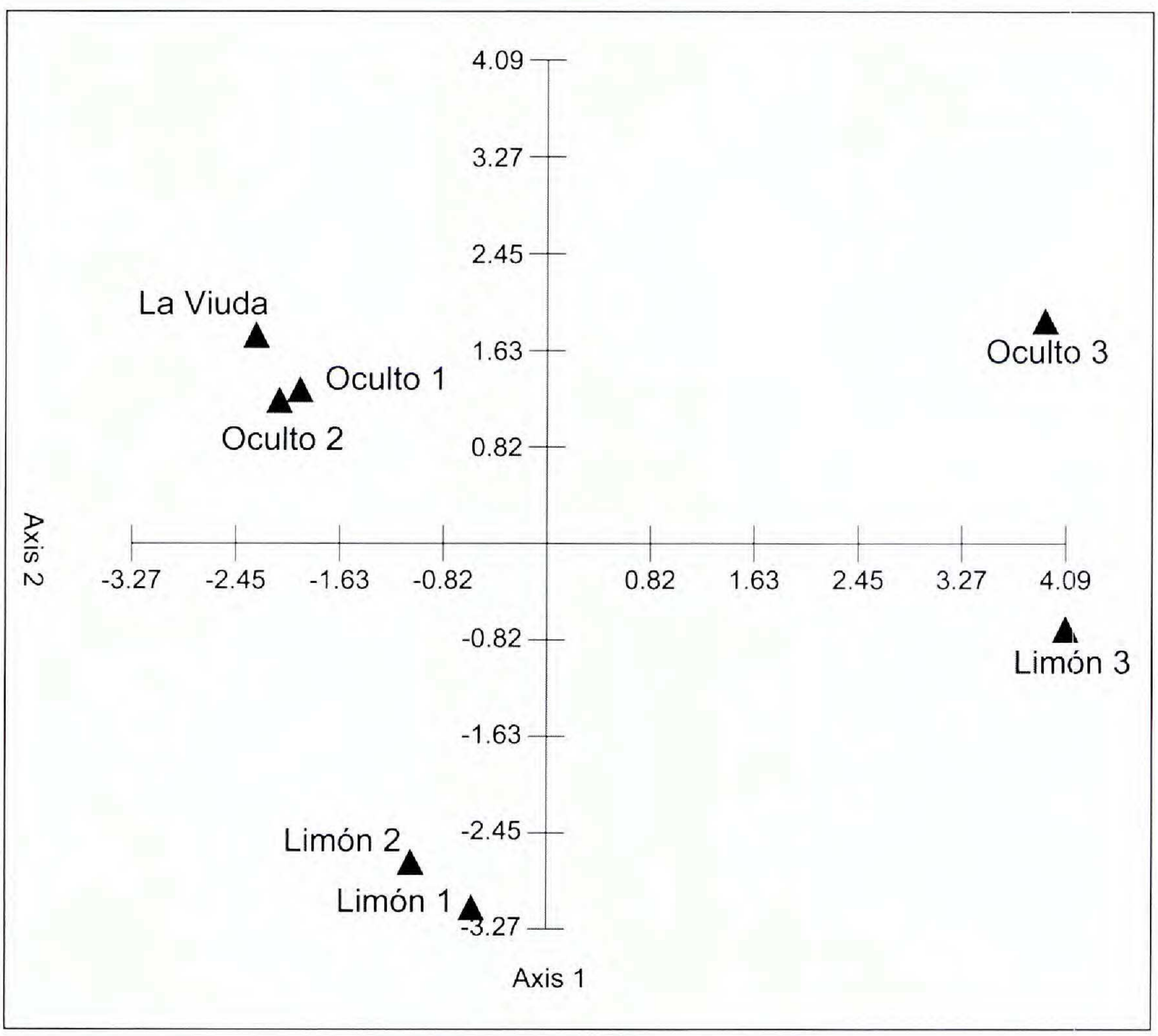

FIG. 2. Ordination of a Principal Component Analysis based on species abundance.

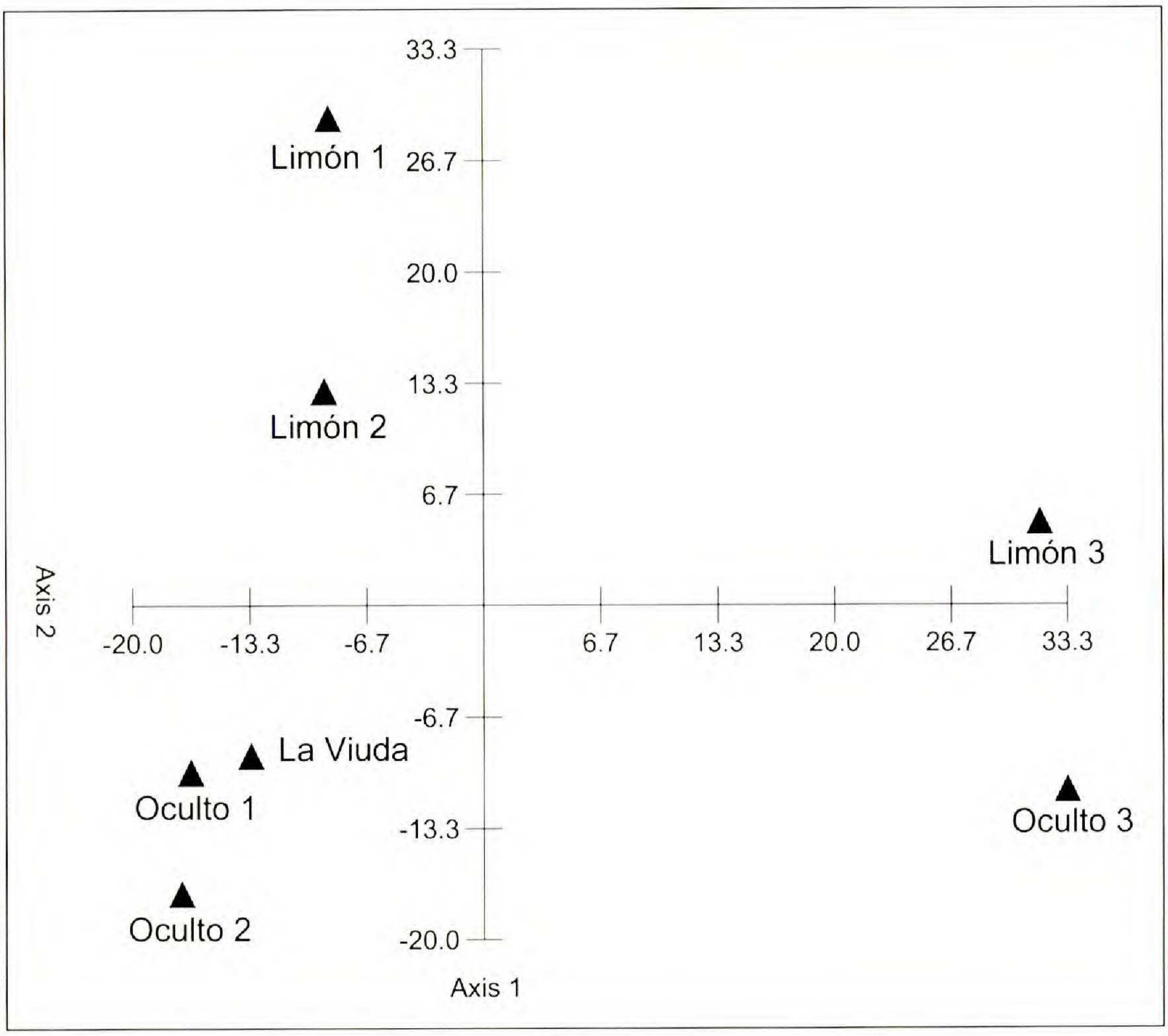

Fig. 3. Ordination of a Principal Component Analysis based on family abundance.

of all species. Table 3 summarizes the Importance Value Index (IVI) for the 20 most abundant families per plot, per forest type, and across all plots, emphasizing the importance of Arecaceae in PS forest plots, and the Fabaceae across all forest plots.

Table 4 lists the twenty most abundant species in each of the seven 1-ha forest plots. There were only seven species that occurred in all seven plots. Twenty species were found to occur in all five TF forest plots while 62 species were found to occur in both of the PS forest plots. A total of 243 species were found to occur in only one plot out of the seven. Out of the total of 442 species found across all the plots, 124 occurred only in the PS forest and 212 only in the TF forest. A total of 106 species were found to occur in both forest types. About 40% of the species were represented by only one individual and 65% by 1 to 3 individuals.

Similarity

Table 5 shows the Sørensen Similarity Index for all plots. Values range from 0.25 to 0.55 for all species and from 0.10 to 0.75 when only the 20 most abundant

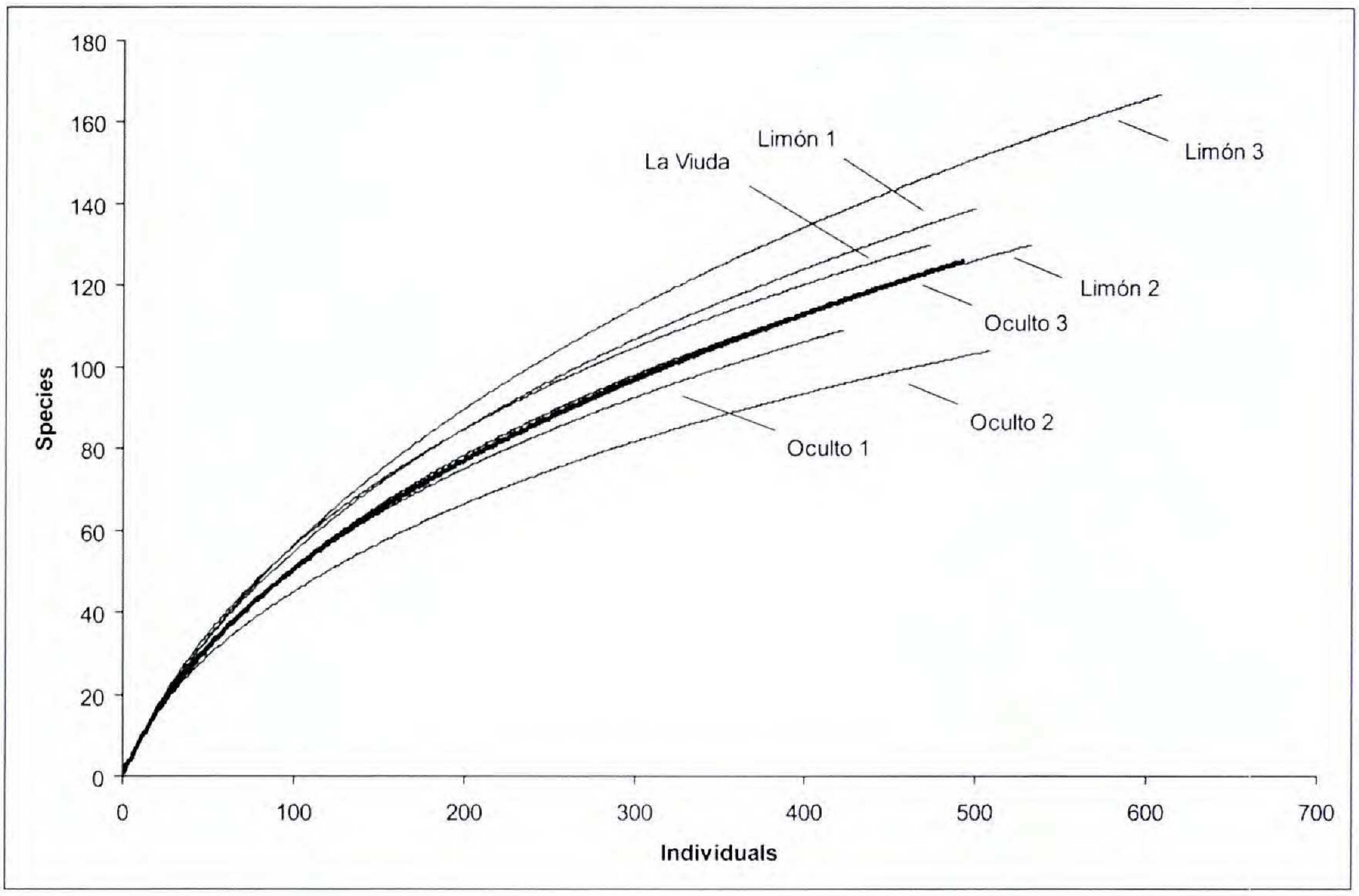

Fig. 4. Rarefaction curve showing relationship between number of individuals and number of species.

species were included. The 20 most abundant species, on average, represent 60% of all individuals (Range: 54–69%). Similarity analysis shows the same patterns already observed in the PCA. First, plots within the same forest type (TF or PS) are more similar to each other. Considering only the 20 most abundant species in each plot, this pattern becomes even more apparent. The TF forest plots from the same site (e.g., Oculto 1 and 2 or Limón 1 and 2) share a higher number of species with each other than they do with plots from different sites. Figure 5 provides the results of WPGMA cluster analysis based on species abundance, which shows that PS forest plots cluster together, as do TF forest plots from the same sites. When all species are considered, PS forests are more similar to the TF forest plots at the same site than to those farther away. However, this is not true when we consider only the 20 most abundant species. In this case, Limón 3 shares the same number of species with Limón 1 as it does with Oculto 2, and Oculto 3 and Oculto 1 are the least similar plots.

DISCUSSION

The Palma Real watershed presents a unique seasonally inundated PS forest habitat that is very different from the TF forests of the region. Based on species abundance, the two PS forest plots are clearly distinguished from the TF forest plots as shown by results of both PCA (Figs. 2, 3) and WPGMA cluster analysis (Fig. 5), as well as similarity index analysis (Table 5). *Euterpe precatoria* is the

TABLE 2. The 20 most diverse families in the two main forest types. Families in boldface are those that are among the top 20 in both forest types. Number of individuals are average by hectare.

Terra firme Forest			palm swamp Forest		
Family	No. of individuals	No. of Species	Family	No. of individuals	No. of Species
Fabaceae	41.6	39	Fabaceae	78	35
Lauraceae	30.6	26	Annonaceae	12	12
Moraceae	26.8	22	Chrysobalanaceae	18	12
Sapotaceae	9.6	17	Lauraceae	7.5	11
Chrysobalanaceae	7.6	14	Sapotaceae	16	11
Meliaceae	12.4	12	Moraceae	33.5	10
Annonaceae	9.4	11	Burseraceae	15.5	8
Cecropiaceae	20.2	10	Arecaceae	128.5	7
Monimiaceae	53	9	Apocynaceae	10.5	7
Flacourtaceae	6	9	Anacardiaceae	11.5	6
Apocynaceae	7.8	7	Lecythidaceae	24	7
Arecaceae	52.8	6	Clusiaceae	10.5	4
Burseraceae	19.8	6	Myrtaceae	15	4
Myristicaceae	36.8	5	Cecropiaceae	7.5	3
Rubiaceae	7.2	4	Meliaceae	8	3
Lecythidaceae	12.4	4	Dichapetalaceae	11.5	2
Violaceae	26.6	2	Violaceae	28.5	2
Linaceae	9.4	2	Ochnaceae	10.5	2
Strelitziaceae	14.2	1	Combretaceae	8	2
Bixaceae	9	1	Sterculiaceae	10	2

most abundant species in PS forest plots, Limón 3 and Oculto 3, contributing significantly to the major differentiation between the PS and TF forest plots. *Astrocaryum murumuru*, *Attalea butyracea*, *Brosimum laevis*, *Chimarrhis sp. 1*, *Dipteryx micrantha*, *Eriotheca globosa*, *Manilkara bidentata*, *Ouratea weberbaueri*, *Rheedia sp. 2*, *Terminalia oblonga*, and *Triplaris americana* are restricted to PS forest plots. *Calyptranthes bipenis*, *Iryanthera juruensis*, Lauraceae sp. 1, Lauraceae sp. 2, *Pourouma minor*, and Rubiaceae sp. 2 are restricted to TF forest plots. Based on our results, there are two groups of TF forest plots as demonstrated by Figures 2, 3, and 5. The first group of TF forest plots, Limón 1 and Limón 2, is distinguished primarily by the abundance of *Brosimum alicastrum*, *Pseudolmedia laevigata*, and *Rinoreocarpus ulei*, and secondarily by *Phenakospermum guyanense*. The second group of TF forest plots, Oculto 1, Oculto 2, and La Viuda, is distinguished by the abundance of *Minquartia guianensis*, *Oenocarpus batua*, *Roucheria punctata*, *Roucheria* sp. 1, Rubiaceae sp. 1, *Socrotea exorrhiza*, and *Tontolea corymbosa*.

Analysis of family abundance demonstrates similar results (Fig. 3, Table 3). The families Fabaceae and Arecaceae are the most abundant families across

TABLE 3. Family Importance Value (FIV) of the 20 most abundant families for each plot, both forest types, and across all plots (sorted by Total column). The FIV was calculated as the sum of relative diversity, relative density, and relative dominance.

Family	LaViuda1	Limón1	Limón2	Limón3	Oculto1	Oculto2	Oculto3	PS	TF	Total
Fabaceae	35.39	33.25	42.05	52.04	25.96	29.65	47.27	48.96	33.55	37.28
Arecaceae	16.76	14.46	17.85	31.91	18.65	22.38	48.26	38.36	16.34	22.32
Moraceae	13.14	36.99	39.55	25.83	9.18	3.01	27.71	27.37	20.48	21.30
Lecythidaceae	20.45	30.71	4.90	17.16	37.98	17.41	9.49	13.45	22.05	20.11
Lauraceae	22.78	21.32	15.84	5.20	23.29	26.39	6.84	6.95	22.39	19.16
Monimiaceae	17.35	13.40	19.64	1.62	20.63	16.20	4.26	3.25	17.65	13.28
Sapotaceae	9.24	12.75	7.45	14.36	8.00	10.78	7.61	11.59	10.56	11.31
Burseraceae	6.26	8.81	10.92	11.01	12.86	15.82	4.53	8.10	10.36	9.52
Myristicaceae	12.42	9.69	6.69	4.46	12.80	24.57	1.41	3.13	12.01	9.17
Cecropiaceae	8.40	11.79	16.22	3.62	9.31	17.03	4.25	3.51	11.63	9.07
Chrysobalanaceae	5.80	5.51	6.06	10.40	9.63	5.73	14.52	12.06	7.26	8.69
Violaceae	2.58	22.93	12.96	13.98	3.11	2.40	4.48	9.40	8.59	8.52
Annonaceae	8.25	5.53	6.62	5.36	4.40	9.50	12.22	8.48	6.96	7.31
Apocynaceae	9.99	8.15	6.98	7.73	6.17	5.81	7.21	7.27	7.20	6.88
Meliaceae	3.40	7.50	14.20	2.41	8.27	9.74	5.59	3.43	8.50	6.74
Euphorbiaceae	5.77	4.33	1.07	5.79	6.56	8.51	3.20	3.89	6.40	5.69
Flacourtiaceae	10.37	0.97	7.12	5.91	7.30	5.65	1.08	3.85	5.92	5.68
Anacardiaceae	2.11	4.99	4.77	5.61	5.23	4.50	8.75	7.25	4.60	5.25
Clusiaceae	6.18	3.71	3.71	5.66	2.90	3.29	3.62	4.43	4.36	4.61

all PS and TF forest plots, although they are more abundant in PS forest plots. The Lauraceae and Monimiaceae are more abundant in TF forest plots. The Violaceae and Moraceae are much more abundant in all the Limón plots including the PS forest plot Limón 3, distinguishing all the Limón plots from the other plots on axis 1 in the PCA (Fig. 3). The Dichapetalaceae and Polygonaceae are found only in PS forest plots, helping to distinguish them from TF forest plots. A higher abundance of the Bombacaceae in PS forest plots also helps to distinguish them from the TF forest plots. The first TF forest plot group of Limón 1 and 2 is distinguished by a higher abundance of Lauraceae species than the rest of the plots, as well as by the Staphylaceae, which only occurs in Limón 1 and 2 TF forest plots. The second TF forest plot group of Oculto 1 and 2 and La Viuda is distinguished by a high abundance of Myristicaceae, as well as by the Bixaceae, Hippocrateaceae, and Linaceae, which only occur in those plots.

PS forest plots of Palma Real have a higher abundance of palms in comparison to the TF forest plots, making the Arecaceae one of the most significant families distinguishing the different forest types (Table 2 & 3). This is especially apparent in Oculto 3, where palms account for the top three and sixth most abundant species sampled. Palms compose 25% of the stems in Oculto 3 and 16% in Limón 3. In comparison, in all TF forest plots in the region palms make up only 9% of all stems. *Euterpe precatoria*, the most common palm in the area,

TABLE 4. The twenty most abundant species in each of the seven one-hectare forest plots.

LaViuda1		Oculto1		Oculto2		Limón1	
Bixa arborea	32	Siparuna decipiens	31	Iryanthera laevis	50	Leonia glycicarpa	40
Siparuna sp. 1	30	Siparuna sp. 1	28	Siparuna sp. 1	35	Rinoreocarpus ulei	40
Siparuna decipiens	19	Euterpe precatoria	27	Iryanthera juruensis	30	Euterpe precatoria	27
Tachigali chrysophylla	17	Iryanthera laevis	19	Euterpe precatoria	29	Siparuna decipiens	23
Oenocarpus bataua	15	Lauraceae sp. 1	16	Tachigali chrysophylla	21	Iryanthera juruensis	20
Socrotea exorrhiza	15	Ouratea sp. 1	16	Lauraceae sp. 1	20	Lauraceae sp. 1	15
Euterpe precatoria	14	Oenocarpus bataua	14	Oenocarpus bataua	18	Pseudolmedia laevis	15
Lauraceae sp. 1	14	Protium sp. 2	12	Pourouma minor	18	Siparuna sp. 1	15
Roucheria punctata	12	Tetragastris panamensis	12	Eschweilera coriacea	17	Brosimum alicastrum	10
Iryanthera juruensis	11	Iryanthera juruensis	10	Phenakospermum guyanense	17	Lauraceae sp. 2	10
Tachigali polyphylla	10	Roucheria punctata	10	Protium sp. 2	17	Guarea macrophylla	7
Calypthrantes bipenis	9	Tachigali polyphylla	10	Socrotea exorrhiza	13	Inga auristillae	7
Tetragastris panamensis	9	Tontolea corymbosa	9	Bixa arborea	12	Lauraceae sp. 9	7
Iryanthera laevis	8	Hirtella glandistipula	8	Siparuna decipiens	10	Pseudolmedia laevigata	7
Melastomataceae sp. 1	7	Bertholletia excelsa	7	Tetragastris panamensis	9	Socrotea exorrhiza	7
Phenakospermum guyanense	7	Pourouma minor	7	Tontolea corymbosa	9	Tetragastris panamensis	7
Pourouma minor	7	Trichilia quadrijuga	7	Ouratea sp. 1	8	Turpinia sp. 1	7
Rubiaceae sp. 2	7	Phenakospermum guyanense	6	Lacistema aggregatum	7	Castilla ulei	6
Inga gereauana	6	Hebepetalum humirifolium	6	Roucheria punctata	6	Celtis schippii	6

TABLE 4 (continued from left)

Limón2		Limón3		Oculto3	
Euterpe precatoria	55	Euterpe precatoria	88	Euterpe precatoria	61
Siparuna decipiens	38	Leonia glycicarpa	32	Socrotea exorrhiza	32
Phenakospermum guyanense	36	Calypthranthes densiflora	26	Astrocaryum murumuru	31
Rinoreocarpus ulei	27	Eschweilera coriacea	26	Tachigali chrysophylla	25
Siparuna sp. 1	25	Tachigali chrysophylla	23	Theobroma subincanum	16
Tetragastris panamensis	22	Socrotea exorrhiza	15	Attalea butyracea	13
Brosimum alicastrum	13	Rinoreocarpus ulei	13	Tapura tessmannii	13
Iryanthera juruensis	12	Ouratea cf. weberbaueri	12	Terminalia oblonga	13
Leonia glycicarpa	12	Tetragastris panamensis	12	Eschweilera coriacea	12
Tachigali sp. 1	11	Neea sp. 8	10	Leonia glycicarpa	12
Pourouma guianensis	10	Brosimun lactescens	9	Brosimun lactescens	11
Lauraceae sp. 1	8	Manilkara bidentata	9	Hirtella excelsa	10
Pourouma minor	8	Tapura tessmannii	9	Triplaris americana	10
Cecropia sciadophylla	7	Inga edulis	8	Dipteryx micrantha	9
Eschweilera coriacea	7	Tachigali polyphylla	8	Tapirira guianensis	8
Pseudolmedia laevigata	7	Aspidosperma vargasii	7	Brosimun guianensis	6
Tachigali sp. 2	7	Chimarrhis sp. 1	7	Cecropia sciadophylla	6
Aspidosperma vargasii	6	Pseudolmedia macrophyla	7	Cordia cf. scabrifolia	6
Geissospermum reticulatum	6	Rheedia sp. 2	7	Inga gereauana	6

TABLE 5. Number of common species (above) and Sørensen Similarity Index (below) by one-hectare plot. The diagonal shows the total number of species for each plot. All species / 20 most abundant species.

	La Viuda	Limón 1	Limón 2	Limón 3	Oculto 1	Oculto 2	Oculto 3
La Viuda	**130**	51 / 8	56 / 10	43 / 5	55 / 13	46 / 13	32 / 4
Limón 1	0.38 / 0.40	**138**	61 / 10	56 / 5	49 / 7	49 / 8	36 / 3
Limón 2	0.43 / 0.50	0.45 / 0.50	**130**	50 / 7	48 / 10	52 / 10	32 / 5
Limón 3	0.29 / 0.25	0.37 / 0.25	0.34 / 0.35	**167**	40 / 4	44 / 5	64 / 8
Oculto 1	0.46 / 0.65	0.40 / 0.35	0.40 / 0.50	0.29 / 0.20	**109**	59 / 15	34 / 2
Oculto 2	0.39 / 0.65	0.40 / 0.40	0.44 / 0.50	0.32 / 0.25	0.55 / 0.75	**104**	33 / 4
Oculto 3	0.25 / 0.20	0.27 / 0.15	0.25 / 0.25	0.44 / 0.40	0.29 / 0.10	0.29 / 0.20	**126**

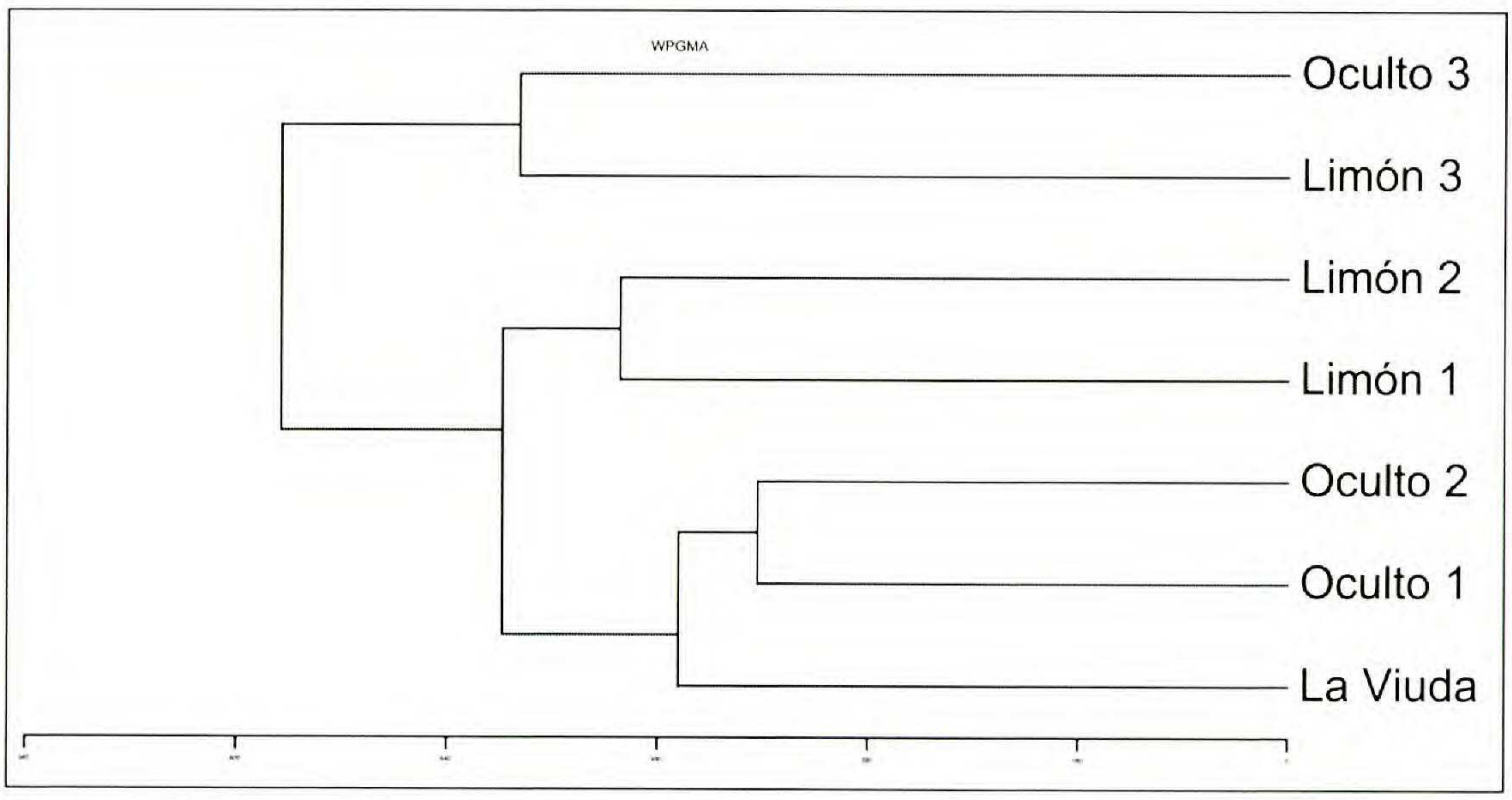

FIG. 5. Dendrogram of WPGMA cluster analysis based on family and species abundance.

is among the five most abundant species in six of the one-hectare forest plots and it is the most abundant species sampled in both of the PS forest plots, with 88 stems in Limón 3 and 61 stems in Oculto 3. *Socratea exorrhiza* is also an important species in PS forest plots, ranking as the sixth most abundant species in Limón 3 with 15 stems, and the second most abundant species in Oculto 3, with 32 stems. *Astrocaryum murumuru* is the third most abundant species in Oculto 3, with 31 stems. In Oculto 3, *Attalea butyracea*, known locally as "shebon", is the sixth most abundant species, from which has come the local common name of this forest type, *shebonal*, but this is not true for Limón 3.

One of the most important families in the TF forest plots was the Monimiaceae (Figs. 2, 3), making this the first report of high abundance and dominance of this family in any tropical forest plot study. This family was rep-

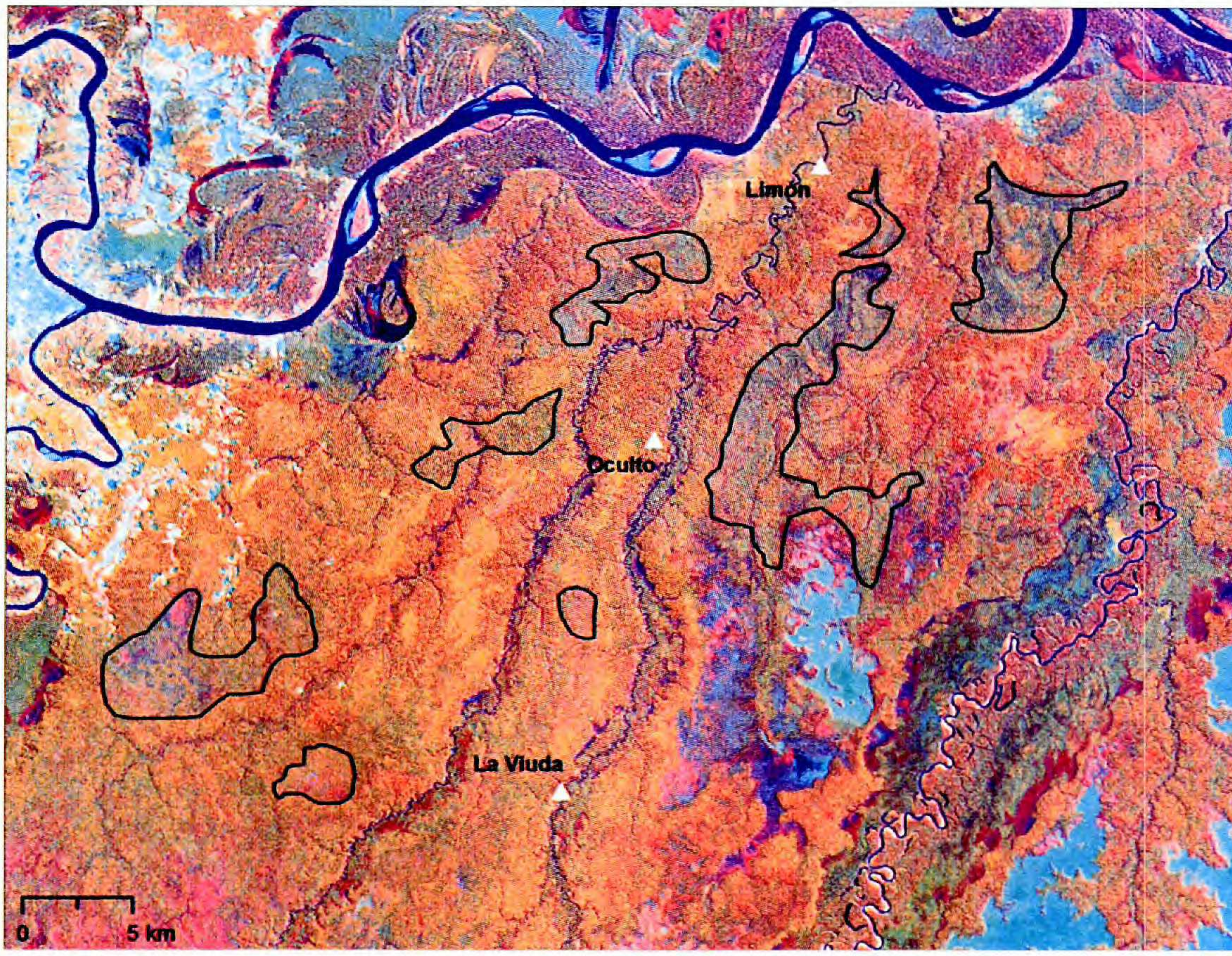

FIG. 6. Landsat TM satellite image from July 2001 showing the three field sites, Limón, Oculto, and La Viuda, and the distribution and extent of palm swamp forests in the region. Bright blue areas to the right are the Pampas del Heath on the border of Peru and Bolivia.

resented by two species of the genus *Siparuna* that were common in areas of tree fall gaps. The presence and abundance of *Tachigali* sp., a monocarpic species of the Palma Real watershed, might explain the presence of tree fall gaps and existence of several groups of light-demanding species (e.g., Brazil nut and Cecropiaceae).

We found that the PS forest plots differ structurally from other forests by a greater number of stems, the distribution of tree diameter size, and basal area, especially the site Limón 3, which has 80 more stems than other plots (Table 1). In contrast, the TF forest plots in the Palma Real watershed present the typical structure in comparison to reports from other regions in Madre de Dios, and the Amazon basin, in general (Pitman et al. 2001).

The PS forests of the Palm Real watershed are characterized by several months of anaerobic conditions because of the inundation of the area during the rainy season from at least November to February. As suggested by Terborgh and Andresen (1998) and Connell and Lowman (1989), who note that swamp forests are characterized by low tree diversity and high dominance by one or a low number of species, we expected to find a relatively low species diversity in the PS forests of the Palm Real watershed. However, the most significant result of this study was that the PS forests in the Palma Real watershed were found to have a higher tree species diversity per unit area than TF forests of the region. Limón 3, a PS forest plot, was the most diverse of all plots sampled, with 167 tree species, only seven species less than the average diversity of 175 species across 14 one-hectare TF forest plots sampled in Madre de Dios, Peru, by Pitman et al. (2001). Although Oculto 3 was not as diverse as Limón 3, with 126 species it had more or just slightly fewer species than the TF forest plots sampled, and it was more diverse than the two neighboring TF forest plots from the same site (Oculto 1 and 2). All of our TF forest plots from the Palma Real watershed were less diverse than TF forest plots sampled in the neighboring Tambopata region, which range between 151 and 197 species (Gentry 1988; Phillips et al. 2003).

It is interesting to compare the diversity of the two PS forest plots of the Palma Real watershed with other one-hectare swamp forest plots in the Madre de Dios region. Pitman et al. (1999) and Terborgh and Nuñez (unpublished data) have found a range of 61–129 tree species among five one-hectare plots in Madre de Dios, Peru. Phillips et al. (2003) report 158 tree species from a swamp forest plot in the Tambopata region. The Oculto 3 PS forest plot from Palma Real falls out at the upper limit of the first range, with 126 species total. Limón 3, with 167 species, appears to be the most diverse swamp forest plot discovered to date in Madre de Dios, Peru. And, as mentioned, Limón 3 is nearly as diverse or is more diverse than many non-wetland TF and floodplain forest plots in Madre de Dios, Peru.

Our results and discoveries lead us to some important questions about the forests of the Palma Real watershed and argue for continued studies of this region. First of all, why are the PS forest plots of Palma Real so high in diversity in comparison to plots in neighboring non-swamp forest plots? And second, why are the TF forest plots relatively low in diversity compared to the PS forest plots of the Palma Real watershed, especially Limón 3, and other TF forest plots from the Tambopata region and Madre de Dios, Peru, in general?

The importance of the PS forest in the region can be seen in the Landsat satellite image (Fig. 6), which shows the great expanse of these forests across the landscape from the Tambopata River in Peru to the Heath River on the Bolivian-Peruvian border and beyond to the east into Bolivia. Preliminary studies in the La Torre River watershed (Cornejo, unpublished data) show a forest with the same characteristics of the PS forests of the Palma Real watershed, with a dominance in the understory of *Lycopodium* sp., *Selaginella* sp., *Clusia* spp., Melastomataceae spp., and other species of non-woody plants that were not sampled in our forest plots. Interestingly, such plants are also found in the vast wetland savannahs to the east, known as the Pampas del Heath along the border of Peru and Bolivia. Local people in the region, in passing conversations with our team, have mentioned that the Pampas del Heath wetland savannahs can develop into dense swamp forests, especially in the absence of management by fire. We hypothesize that these diverse PS forests may represent a successional stage of vegetation derived from the Pampas del Heath savannahs that are more common to the east. This hypothesis could be tested using a combination of remote sensing and intensive ground-truthing between the Tambopata region and the Pampas del Heath savannahs to the east. The Pampas del Heath sits on a thick mass of organic matter that has accumulated over hundreds of years of deposition and slow decomposition characteristic of wetland ecosystems (i.e., bogs). In other words, perhaps the scattered PS forests of the Palma Real watershed and surrounding region represent a preliminary stage of succession from open wetland savannah to tropical forest. Pollen cores could shed some light on the succession of these vegetation types.

This leads us to our second open-ended question, which is why are the TF forest plots of the Palma Real relatively low in diversity? The forests of Madre de Dios, Peru, are referred to as subtropical moist tropical forests (Foster et al. 1994). It is possible that the forests in the Palma Real watershed receive less precipitation than forests to the west, from Tambopata to Manu, in Madre de Dios, Peru. However, there are no climate data available to test this hypothesis. Another possibility is that the soils of TF forests in the Palma Real region are nutrient-poor. We do not have data that enable us to test this hypothesis. We recommend future soil sampling in association with vegetation studies in the Palma Real region.

It is possible that with continued sampling of PS and TF forests in the Palma Real watershed, other patterns of plot diversity will be discovered, including more diverse TF forests and differences in PS forest diversity. Clearly, more studies are needed of PS and TF forests of the Palma Real watershed. Considering that the Palma Real watershed is one of the most important zones of Brazil nut extraction in all of the southwestern Amazon, we conclude by arguing for more sustained and long-term studies of the botanical and ecological diversity, and the conservation and management of this region.

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REFERENCES

Beck, S.G. 1984. Comunidades vegetales de las sabanas inundazides en el NE de Bolivia. Phytocoenologia 12(2/3):321–350.

Colwell, R.K. 2005. Estimates: Statistical estimation of species richness and shared species from samples. Version 7.5. URL: http://purl.oclc.org/estimates.

Connell, J.H. and M.D. Lowman. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. Amer. Naturalist 134:88–119.

Foster, R., et al. 1994. The Tambopata-Candamo Reserved Zone of southeastern Perú: a biological assessment. RAP Working Papers, Vol 6. Conservation International.

Gentry, A.H. 1988. Tree species richness of upper Amazonian forests. Proc. Natl. Acad. Sci. 85:156–159.

Gotelli, N.J., and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Letters 4:379–391.

Haase, R. 1990. Plant communities of a savanna in northern Bolivia II. "palm swamp"s, dry grasslands, and shrubland. Phytocoenologia 18(2/3):343–370.

Kalliola, R., M. Puhakka, J. Salo, H. Tuimisto, and K. Ruokolainen. 1991. The dynamics, distribution, and classification of swamp vegetation in Peruvian Amazonia. Ann. Bot. Fennici 28:225–239.

Kvist, L.P. and G. Nebel. 2001. A review of Peruvian flood plain forests: ecosystems, inhabitants, and resource use. Forest Ecol. Managem. 150:3–26.

Nebel, G., L.P. Kvist, J.K. Vanclay, H. Christensen, L. Freitas, and J. Ruiz. 2001. Structure and floristic composition of flood plain forests in the Peruvian Amazon I. Overstorey. Forest Ecol. Managem. 150:27–57.

Oliveira, A.D. de and S.A. Mori. 1999. A central Amazonian terra firme forest. I. High tree species diversity on poor soils. Biodivers. & Conservation 8:1219–1244.

Phillips, O.L., R. Vásquez Martinez, P. Nuñez Vargas, A. Lorenzo Monteagudo, M. Chuspe Zans, W. Galiano Sánchez, A. Peña Cruz, M. Timaná, M. Yli-Halla, and S. Rose. 2003. Efficient plot-based floristic assessment of tropical forests. J. Trop. Ecol. 19:629–645.

PITMAN, N.C.A., J. TERBORGH, M.R. SILMAN, and P. NUÑEZ V. 1999. Tree species distributions in an upper Amazonian forest. Ecology 80:2651–2661.

PITMAN, N.C.A., J.W. TERBORGH, M.R. SILMAN, P. NUÑEZ V., D.A. NEILL, C.E. CERÓN, W.A. PALACIOS, and M. AULESTIA. 2001. Dominance and distribution of tree species in upper Amazonian "terra firme" forests. Ecology 82:2101–2117.

TERBORGH, J.W. and E. ANDRESEN. 1998. The composition of Amazonian forests: patterns at local and regional scales. J. Trop. Ecol. 14:645–664.

TER STEEGE, H., D. SABATIER, H. CASTELLANOS, T. VAN ANDEL, J. DUIVENVOORDEN, A.A. DE OLIVEIRA, R. EK, R. LILWAH, P. MAAS, and S.A. MORI. 2000. An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. J. Trop. Ecol. 16:801–828.

TER STEEGE, H., N.C.A. PITMAN, D. SABATIER, H. CASTELLANOS, P. VAN DER HOUT, D.C. DaKy, M. SILVEIRA, O. PHILLIPS, R. VASQUEZ, T. VAN ANDEL, J. DUIVENVOORDEN, A.A. DE OLIVEIRA, R. EK, R. LILWAH, R. THOMAS, J. VAN ESSEN, C. BAIDER, P. MAAS, S.A. MORI, J. TERBORGH, P. NUÑEZ VARGAS, H. MOGOLLÓN, and W. MORAWETZ. 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. Biodivers. & Conservation 12:2255–277.

VALENCIA, R., H. BALSLEV, G. PAZ, and C. MIÑO. 1994. High tree alpha-diversity in Amazonian Ecuador. Biodivers. & Conservation 3:21–8.